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The role of Eurasian beaver (*Castor fiber*) in the storage, emission and deposition of carbon in lakes and rivers of the River Ob flood plain, western Siberia

Roberto Cazzolla Gatti [a,*], Terry V. Callaghan [a,e], Inna Rozhkova-Timina [a], Anastasia Dudko [b], Artyom Lim [a], Sergey N. Vorobyev [a], Sergey N. Kirpotin [a], Oleg S. Pokrovsky [c,d]

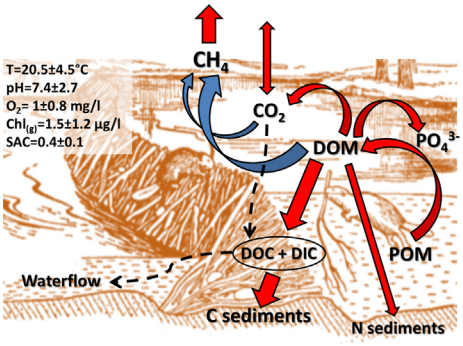
[a] Bio-Clim-Land Centre, Biological Institute, Tomsk State University, Tomsk, Russia
[b] Department of Geoecology and Geochemistry, Institute of Natural Resources, Tomsk Polytechnic University, Tomsk, Russia
[c] GET UMR 5563 CNRS, 14 Avenue Edouard Belin, 31400 Toulouse, France
[d] IEPS, Federal Centre for Integrated Arctic Research, 23 Naberezh Sev Dviny, 163000 Arkhangelsk, Russia
[e] Department of Animal and Plant Sciences, The University of Sheffield, Western Bank, Sheffield S10 2TN, UK

HIGHLIGHTS

- The impact of carbon emissions from wetlands on climate change has been recently emphasised
- Beavers (*Castor spp.*) influence the biogeochemical cycling of carbon by creating conditions for sediment accumulation in streams and methanogenesis.
- We assessed the impact of Eurasian beavers on the whole carbon-related of the Ob river's effluent floodplain streams in Western Siberia
- We compared dammed and free water courses and discussed the results in the light of their importance on the global carbon cycle
- We now have a strong evidence that beavers increase the aqueous concentration of methane by building their dams
- We also show that, simultaneously, they act as nutrient recyclers and as potential carbon sequesters, accumulating C into the sediments and thus subtracting it from the short-term carbon cycle
- This should be taken into consideration in river management and as a further reason for the conservation of beaver species

GRAPHICAL ABSTRACT

The processes of carbon-related parameters in ponds created by beaver dams. The dimension of the arrows indicates the strength of the process. Red arrows are both aerobic and anaerobic processes and blue arrows are obligatory anaerobic processes. The strength of the relation between CO_2 and DOC is still debated. Mean values ± standard deviation of the significant parameters recorded in the beaver ponds of the river Ob are reported in the figure.



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ABSTRACT

Several studies have reported significant emission of greenhouse gasses (GHG) from beaver dams, suggesting that ponds created by beavers are a net source of CO_2 and CH_4. However, most evidence come from studies conducted in North America (on *Castor canadensis*) without a parallel comparison with the Eurasian beaver's (*Castor fiber*) impacts and a critical consideration of the importance of the carbon deposition in dam sediments. The most

* Corresponding author.
E-mail address: robertocazzollagatti@mail.tsu.ru (R. Cazzolla Gatti).

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abundant population of the Eurasian beaver lives in Russia, notably within the River Ob watershed in Western Siberia which is the second largest floodplain on Earth. Consequently, we assessed the holistic impact of Eurasian beavers on the multiple carbon pools in water and on other related biogeochemical parameters of the Ob's floodplain streams. We compared dammed and flowing streams in a floodplain of the middle course of the river. We found that beavers in western Siberia increase the stream emission of methane by about 15 times by building their dams. This is similar to what has been documented in North America. A new finding from the present study is that Siberian beavers facilitate 1) nutrient recycling by speeding up the nutrient release from particulate organic matter; and 2) carbon sequestration by increasing the amount of dissolved organic carbon. This carbon becomes in part recalcitrant when buried in sediments and is, therefore, removed from the short-term carbon cycle. These new results should be taken into consideration in river management and provide a further reason for the conservation and management of Eurasian Beavers.

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1. Introduction

The impact of carbon emissions from wetlands on climate change has recently been emphasised (Mitsch and Mander, 2018). The role of inland water ecosystems within the budget of the global carbon cycle is now better integrated into ecological and biogeochemical theory (Cole et al., 2007; Banerjee et al., 2016; Messina et al., 2016) but is not completely included in climate models. This lack of integration applies especially to northern and boreal ecosystems that exert strong feedback effects on the climate system (Serreze and Francis, 2006) and, to some extent, redresses the imbalance as, so far, most studies have focused on the role of methane emissions in the global GHG cycle (Bastviken et al., 2011). There is an increasing interest in the fact that the contribution of CH_4 to climate forcing during the past 150 years is about 35% of the climate forcing by CO_2 (Christensen et al., 2003; AMAP, 2015).

In the management of freshwater basins, a controversy emerged about the greenhouse gas emissions derived from hydroelectric dams. This controversy led to a rethinking of the supposedly "clean energy" hydroelectric source. It seems, in fact, that when the water emerges from the turbines of a dam, there is sizeable CH_4 and CO_2 evasion to the atmosphere (Fearnside, 2004; Cazzolla Gatti, 2016a, 2016b). Similarly, in natural ecosystems, beaver (*Castor* spp.) dams influence the biogeochemical cycling of carbon by creating conditions for sediment accumulation in streams and providing anoxic environments suitable for significant methanogenesis (Giriat et al., 2016; Puttock et al., 2017). In a study by Ford and Naiman (1988), the methane evasion was 33-fold greater in beaver ponds than in flowing streams. Accordingly, Weyhenmeyer (1999) reported that net methane fluxes in beaver ponds were moderate to high when compared to other wetland types in the low boreal forest region.

Other authors also showed that beaver ponds are a large source of CO_2 and CH_4 and they can release >200 g C m^{-2} $year^{-1}$ (Yavitt et al., 1992; Roulet et al., 1997; Bubier et al., 1993; Pokrovsky et al., 2012). In the case of methane flux, soil and sediment moisture saturation seems to be the key determinant of high emissions, and when the ground is saturated, differences in emissions between dammed and not dammed streams could be explained by peat and sediment temperatures (Roulet et al., 1992).

Some authors even suggested that about 1% of the recent rise in atmospheric methane may be attributable to pond creation by beavers in North America (Naiman et al., 1991; Bubier et al., 1993). The net methane emission during the ice-free season (May–October) from a beaver-meadow complex is 8–11 g C m^{-2} in the permanently waterlogged zones and 0.2–0.4 g C m^{-2} from the occasionally inundated meadow and forest sites. In a study from the North-eastern USA, it was shown that the shallowness of the beaver ponds may have limited the degree of CH_4 oxidation thus increasing overall CH_4 emissions to the atmosphere (Lazar et al., 2014).

Most of the evidence of GHG emissions from beaver dams comes from studies conducted in North America, specifically, on *Castor canadensis*, without a parallel comparison with the Eurasian beaver's (*Castor fiber*) effects, However, the importance of C sequestration in beaver dams has apparently not been reported. It is important to fill this knowledge gap as we now have a good knowledge of the world distribution of Eurasian beaver (Ye et al., 2018) and the distribution of the introduced American beaver (Halley and Rosell, 2003), and we can even predict beaver abundance responses to projected climatic and biodiversity changes (Jarema et al., 2009; Cazzolla Gatti, 2017; Cazzolla Gatti et al., 2017). Since the most abundant population of the Eurasian beaver lives in Russia, notably within the River Ob watershed (Collen and Gibson, 2000), we assess in this paper the holistic impact of Eurasian beavers on carbon-related variables (CH_4, CO_2, Total Organic Carbon [TOC], C in the sediments and plant biomass) and other related biogeochemical parameters. Our approach is to determine the importance of C emission and burial mediated by beavers by comparing dammed and free watercourses of a flood zone of the River Ob in western Siberia. We discuss the results in the light of the global carbon cycle.

2. Materials and methods

2.1. Study-site description

The River Ob is a major river in western Siberia. It is formed in Altai Mountains by the confluence of the Biya and Katun rivers. The Ob is the world's seventh longest river (3650 km) and it is the largest Arctic river in terms of watershed area, with an average annual discharge of 12,475 m^3 $s^{-1}$and a drainage area of 2,990,000 km^2. The Gulf of the Ob is the world's longest estuary (the 800-km-long, 30 to 80 km wide bay of the Kara Sea). The Ob's floodplain is tens of km wide and is characterised by many tributaries and oxbow lakes (Rozhkova-Timina et al., 2016). This floodplain is the second largest globally, the largest being that of the River Amazon (Varzea, Viers et al., 2005).

The vast floodplain of the Ob may be considered as the major regulator of dissolved carbon and related element transport from the land to the Arctic Ocean (Callaghan et al., 2010; Vorobyev et al., 2015). The majority of the Ob's watershed is situated within the highly productive boreal taiga zone and surrounding bogs, where significant C sequestration occurs. The productivity of the terrestrial boreal biome is highest in the riparian zone and river banks, especially in the permafrost-free region (Huston and Wolverton, 2009).

The middle course of the River Ob is located within the boreal taiga biome (Fig. 1), and includes (i) isolated and interconnected water bodies, flooded during the spring period, but persistent during the base flow (called hereafter "flood lakes"); (ii) the flooded area of the river valley and the first terrace, covered by the river during high flow in May and extending, via a system of interconnected shallow ephemeral lakes and primary and secondary water channels, over 5–10 km from the main water channel (called the "flood zone"); and finally (iii) "small rivers" that are small, first-order tributaries of the River Ob, having a watershed area of 10 to 100 km^2 and draining both the terraces and the flood zone.

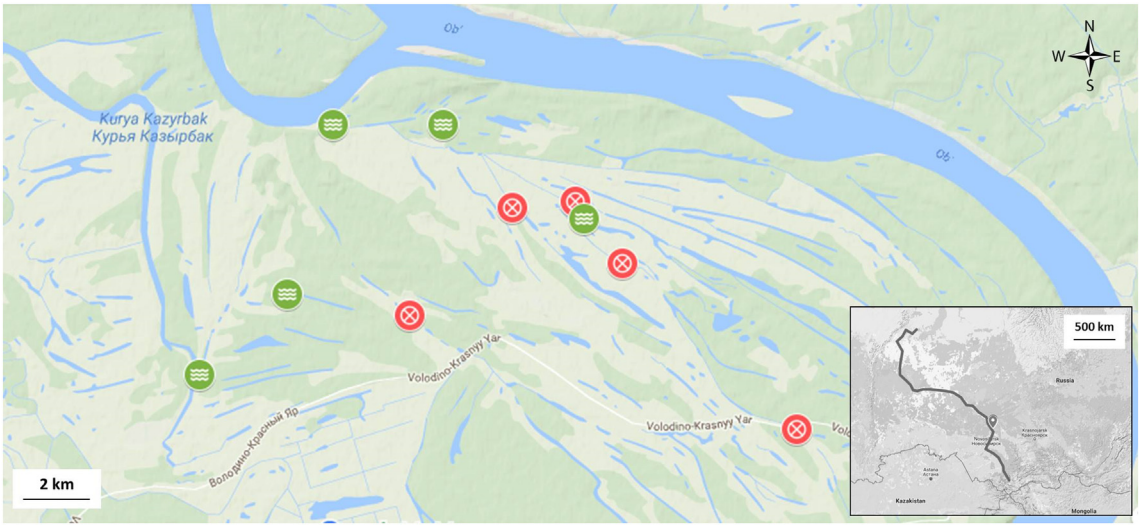

Fig. 1. Study location map. The dark line in the small picture is the area covered by the course of the River Ob in Western Siberia, from its source in the Altai Mountains to its delta in the Kara Sea; the study sites are shown on the large map of the floodplain: green points are free-flowing streams without beaver dams and red points are streams dammed by beavers (centroid coordinates of the study area: 57°13′3.04″N; 84°12′32.46″E).

2.2. Beaver populations in the study area and field data collection

The literature about the beaver population in the middle course of the River Ob is unavailable. However, according to our estimates from an area of 30 km^2in our study site, we expect to find about 10 beaver dams and about 15 groups, each of composed of 5–8 individuals. Approximating the River Ob floodplain to 20 ± 10 km wide and 1000 km long (=20,000 ± 10,000 km^2), and assuming 10 dams/30 km^2 (0.33 dams/km^2), we estimate the number of beaver ponds in the whole middle course of the River Ob as 6600 ± 3300. About 5–6 thousand beavers have been estimated to occur in the Tomskya region (316,900 km^2 area) and 13,000–19,000 in the Kemerovska region (95,500 km^2 area) (Zavyalov et al., 2005) which are regions partially included in our study area.

We also documented the removal of about 10 ± 5 trees (mostly belonging to *Populus* and *Salix* species) with a mean d.b.h. of 15 ± 6 cm within an area of 500 m radius surrounding each beaver pond, within our study sites. These trees were felled and likely used by beavers as food and to build their dams.

During the 2016 flood season (April/May), we identified, firstly by satellite maps and then by field survey, 5 floodplain streams (13 ± 1.7 m long and 10 ± 2.2 m wide) with signs of beavers' activities and 5 comparable floodplain streams without any beaver dam and signs of presence. We also confirmed the historical presence/absence of beaver dams in the selected streams by consulting local people and hunting authorities. Because the selected streams were spatially separated and independent (without any among-stream link apart from that with the main River Ob), we considered the 5 dammed (Fig. 2) and 5 undammed streams as five replicates of the two conceptual treatments (beaver dam vs. no-beaver dam).

At the end of the 2016 flood (end of June) we re-confirmed the presence of five complete dams in the selected streams and the absence of obstructions in the other five. Every two weeks during the 2016 completely ice-free months we collected water samples at 0.5 m depth from the water surface ensuring comparable weather conditions (insolation, air temperature and humidity). From the end of June to the end of September, the number of samplings were 7 per 3 subsamples each [n = 21], per 5 replicates [n = 105] per 2 treatments [n = 210]. We measured various relevant parameters (listed below) in all replicates of the two treatments. We also measured water flow velocity in all sites with and without beaver dams by an OTT Hydromet current meter. We found that water velocity is, on average, three-fold higher in undammed streams than in beaver ponds, where dams significantly ($P < 0.05$) reduce the waterflow.

2.3. Carbon-related parameters

We measured both the flux and dissolved concentration of CO_2 across each of the ponds (created by the beaver dams) and the undammed streams by floating in a dinghy to the middle of them. We used a data-logger with an underwater sensor (GM70 Hand-Held Carbon Dioxide Meter, Vaisala®) to measure the dissolved CO_2 at a 2 m depth. Surface water pCO_2 was measured in-situ by deploying a hand-held infrared gas analyzer (IRGA, GMT222 CARBOCAP® probe, Vaisala®; accuracy ± 1.5%) enclosed within a waterproof, gas-permeable membrane. The sensor (with 2000 and 10,000 ppm ranges) was allowed to equilibrate for approximately 10 min to achieve stable readings (within ±10%). We waited for the saturation point to be reached before reading the final value.

To measure the flux of carbon dioxide, we utilised a coupled system composed of the same data logger and sensor (Vaisala®) used for measuring the dissolved CO_2 and a plastic chamber (an insulated bowl) connected to the probe by tubes and left floating into the middle of the river by a fishing pole (Fig. 2). The pCO_2 accumulation rate inside the chamber was recorded continuously at 10 s intervals for 15 min. Replicates of the measurements were obtained 3 times on the stream and lake open surface areas that were free of macrophytes. The CO_2 accumulation curve in the air space of the floating chamber was recorded. The accumulation followed a saturation curve from which we derived the flux of CO_2.

We repeated each measure 3 times (sub-samples) per replicate site and estimated the mean ± standard error values.

Unfiltered water was sampled in 25-ml Serum borosilicate bottles, closed without air bubbling using vinyl stoppers and aluminium cups. The samples were immediately stabilised to stop microbial activity by adding 0.2 ml of saturated $HgCl_2$ using a two-way needle system. In the laboratory, a headspace was created by displacing approx. 40% of the water with N_2 (99.999%). Two 0.5-ml replicates of the equilibrated headspace were analysed for their concentrations of CH_4 and CO_2 using a Bruker GC-456 gas chromatograph (GC) equipped with flame ionisation and thermal conductivity detectors. After every 10 samples, a calibration of the detectors was performed using Air Liquid gas standards (i.e., CH_4 = 145 ppmv and CO_2 = 3000 ppmv). Duplicate injection of the samples showed that the results were reproducible within

Fig. 2. Study sites. A dammed stream (upper left) created by the European beaver (*Castor fiber*; illustrated in the small) of the River Ob basin (photo courtesy of S. N. Kirpotin). Study sites and measurement method. The coupled measurement system used in this research (upper right) consisting of a logger/sensor and a floating chamber to measure CO_2 fluxes (photo courtesy of R. Cazzolla Gatti). A flowing stream (below without beaver dams) (photo courtesy of O. S. Pokrovsky).

±5%. The specific gas solubility for CH_4 (Yamamoto et al., 1976) and CO_2 (Weiss, 1974) were used for the calculation of the total CH_4 and CO_2 content in the vials and this was converted to μmol/L of the initial waters.

The water samples were filtered on-site in pre-washed 30-ml polypropylene Nalgene® flagons by Minisart single-use filter units (0.45 μm pore size, Sartorius, acetate cellulose filter). The first 20 ml of filtrate was discarded. Blanks were used to control the level of pollution induced by sampling and filtration. The dissolved organic carbon (DOC) blanks of filtrate never exceeded 0.1 mg/L. Water pH was measured in the field using a combined electrode with an uncertainty of ±0.02 pH units. DOC and DIC were analysed using a Carbon Total Analyzer (Shimadzu TOC VSCN) with an uncertainty better than 3%. The instrument was calibrated for analysis of both forms of dissolved carbon in organic-rich, dissolved inorganic carbon (DIC)-poor waters (e.g., Prokushkin et al., 2011).

Carbon (C) concentrations were measured in sediments by a "ThermoFlash 2000 NC soil" after dry combustion at 900 °C and Cu catalysis. Sediment samples were collected with a known-volume cylinder up to a depth of 50 cm and cut into layers 10 cm thick.

Finally, we estimated the aquatic, shoreline and terrestrial plant biomass. Aquatic macrophyte biomass was collected using grapnel surveys (Hill, 2005). Ten samples were obtained at each sampling station, with the use of a small 7 cm grapnel on a cord. To estimate the shoreline biomass, we used the rake method (Hill, 2005) by throwing out a line of 10 m along one side of the pond and stream shore. Terrestrial biomass was estimated by collecting with a sickle all herbs, shrubs and grasses in a 2 × 2 m frame in three randomly placed sub-plots at a distance of 5 m from each other, and 5 m from the shore (along one shoreline). In all cases, we counted the number of collected species and weighed the oven-dry (60 °C for 48 h) above-ground biomass of the total samples per site.

2.4. Related biogeochemical parameters

For a better interpretation of our carbon-related results, we collected relevant water biogeochemical parameters. Temperature, conductivity, pH and dissolved oxygen were measured by a WTW Multi3320 pH-Electrode SenTix® 41 and WTW TetraCon 325 CellOx 325data-logger, at a depth of 2 m in the middle of each replicate stream.

Water turbidity was measured with the classical Secchi disk method (Secchi, 1864). Bacterial turbidity (at a wavelength optical density of 600 nm) and the Spectral Absorption Coefficient (SAC) at ƛ254 nm,

were used for estimating the dissolved organic load. We analysed three water samples per site directly in the field with a portable spectrometer in a 1-cm quartz cuvette (Eppendorf BioSpectrometer®). The UV absorbance of the filtered samples was measured at 254 nm using a quartz 10-mm cuvette on an Eppendorf BioSpectrometer®. The specific UV-absorbency ($SUVA_{254}$, L mg^{-1} m^{-1}) was used as a proxy for aromatic C, molecular weight and source of DOM (Weishaar et al., 2003; Ilina et al., 2014 and references therein).

Water content of blue, green and brown (i.e. cyanobacteria, green algae and diatoms/dinoflagellates) chlorophyll was analysed with a fluorescence method using a PHYTO-PAM, Phytoplankton Analyzer System (Walz®) directly after sampling. The calibration of the instrument was performed on aqueous suspensions of monocultures of cyanobacteria, green algae and freshwater diatoms. The average uncertainty of this method was 20%.

Orthophosphate (PO_4^{3-}) was measured in unfiltered samples in a 50-mm cuvette, immediately after the sampling, with a spectrophotometer at 690 nm, with an uncertainty of 15% (Lurie, 1971) following the ascorbic acid method using coloured antimony-phospho-molybdate complex (Neal et al., 2000).

Particulate nitrogen (N) concentration in the sediments, collected with a known-volume cylinder up to a depth of 50 cm, was measured by a "ThermoFlash 2000 NC soil" after dry combustion at 900 °C and Cu catalysed.

Biochemical Oxygen Demand after 5 days (BOD_5) was calculated by standard methods (Delzer and McKenzie, 1999) as the measured difference between the initial (immediately after sampling) and the final (after 5 days of controlled incubation at 20 °C in the darkness) oxygen concentration. This was measured directly with a BOD Sensor.

2.5. Data analysis

In order to evaluate significant statistical differences between the parameters of the two treatments (dammed vs. undammed streams), we performed a preliminary analysis (with R software, "Package glm2"; R Core Team (2017)) using a generalised linear model (GLM) to check the existence of a logistic regression between the dammed/undammed streams (as the dependent variable) and the C-related parameters (as the independent variables). We had as a result a quasi-perfect separation of the dependent variable in the target variables (even after performing a penalized regression). We also expect that this perfect separation is not just a by-product of our sample, but could be true in the natural systems analysed. Therefore, we used the separating variable (i.e. Dam vs. No Dam) simply as the sole predictor for our outcome, not employing a model of any kind.

Therefore, a "small samples non-parametric Mann-Whitney *U* test" was performed (Table 1). A significant difference was set at $P < 0.05$ and highly significant difference at $P < 0.01$.

3. Results

The comparative analysis of carbon-related parameters (Fig. 3 and Table 1) shows that dissolved methane, dissolved carbon dioxide, dissolved organic carbon, carbon in the sediments and shoreline biomass are significantly higher (M-W *U* values in Table 1, $P < 0.05$) in streams with the beaver dams.

In particular, CO_2 dissolved in free streams is about a third of that in beaver ponds; the DOC in beaver ponds is two times greater than in beaver-free streams; dissolved CH_4 in beaver ponds is twenty times greater than in free streams; the carbon concentration of the sediments in beaver ponds is almost twice than in free streams; and shoreline biomass along beaver ponds is four times greater than in free streams. In contrast to these differences related to beaver activity, both terrestrial and aquatic biomass, carbon dioxide flux, and dissolved inorganic carbon show no significant difference.

The comparative analysis of related parameters (Fig. 4 and Table 1) shows that pH, temperature, dissolved oxygen, BOD_5, turbidity depth and green algal chlorophyll are significantly (M-W *U* values in Table 1, $P < 0.05$) higher in streams without the presence of beaver dams, while phosphate concentration in water, nitrogen concentration in the sediments and SAC are higher in dammed streams (M-W *U* values in Table 1, $P < 0.05$). In contrast, conductivity, bacterial concentration (turbidity at optical density, OD, 600 nm) and red-brown algae chlorophyll show no significant difference (M-W *U* values in Table 1, $P < 0.05$).

4. Discussion

4.1. Dams as net sources of GHG and sizable sinks of C

The majority of studies carried out so far agree that dams, both natural (built by beavers) and artificial (built for hydropower purposes), are a net source of methane (Li and Lu, 2012). Thus, in natural ecosystems, the continuous range expansion and growth of the beaver population are considered to be a driver of further increases in CH_4 emissions (Whitfield et al., 2015). Moreover, it is well known that nutrient loading (which we also detected in ponds created by beavers'

Table 1
Biogeochemical and biological parameters and their significance (where $P < 0.05$ are marked with an *).

	Parameter	Mean ± S.E. Dam	Mean ± S.E. No Dam	M-W test (*U*)	P-value
Carbon-related parameters	Dissolved CO_2 (ppm)	8484 ± 879.19*	2758 ± 510	0	0.005963*
	Flux CO_2 (μmol/m^2s)	646 ± 55.37	712 ± 156	10	0.337587
	Dissolved CH_4 (μmol/l)	15.26 ± 1.75*	0.75 ± 0.39	0	0.006093*
	DIC (ppm)	27.5 ± 4.35	22.28 ± 1.79	6	0.105038
	DOC (ppm)	10.35 ± 1.00*	5.89 ± 1.19	2	0.018357*
	Biomass (terrestrial) (g_{dry}/m^2)	260 ± 28	292 ± 94	12	0.5
	Biomass (aquatic) (g_{dry}/m^2)	86. 56 ± 4.16	25.8 ± 2.27	8	0.200983
	Biomass (shoreline) (g_{dry}/m^2)	64.3 ± 13.9*	16.25 ± 6.31	1	0.010786*
	Carbon in sediments (%/g_{dry})	4.30 ± 2.63*	2.76 ± 2.14	14	0.003497*
Ancillary parameters	T (°C)	20.5 ± 2.0	24.8 ± 2.2*	0	0.005834*
	BOD_5 (mg/l)	0.1 ± 0.26	0.45 ± 0.20*	0	0.006093*
	pH	7.39 ± 1.22	8.30 ± 1.29*	0	0.006093*
	Chlorophyll (brown) (μg/l)	10.14 ± 3.45	4.57 ± 0.26	5	0.071836
	Chlorophyll (green) (μg/l)	1.53 ± 0.55	4.48 ± 0.95*	4	0.045344*
	P (PO_4^{3-}) (mg/l)	0.14 ± 0.02*	0.02 ± 0.01	0	0.006093*
	Nitrogen in sediments (%/g_{dry})	0.25 ± 0.15*	0.19 ± 0.14	25	0.031347*
	Dissolved O_2 (mg/l)	1.01 ± 0.45	3.76 ± 0.87*	0	0.006093*
	Conductivity (μS/cm)	230.0 ± 6.8	218 ± 6.6	10	0.338052
	$SUVA_{\lambda 254}$ (100 * SAC / DOC) (abs/m)	0.43 ± 0.29*	0.22 ± 0.21	3	0.030051*
	Water turbidity depth (cm)	64 ± 24.7	134 ± 21.0*	3	0.030051*
	Bacterial turbidity OD600 (nm)	0.02 ± 0.01	0.08 ± 0.06	11	0.417266

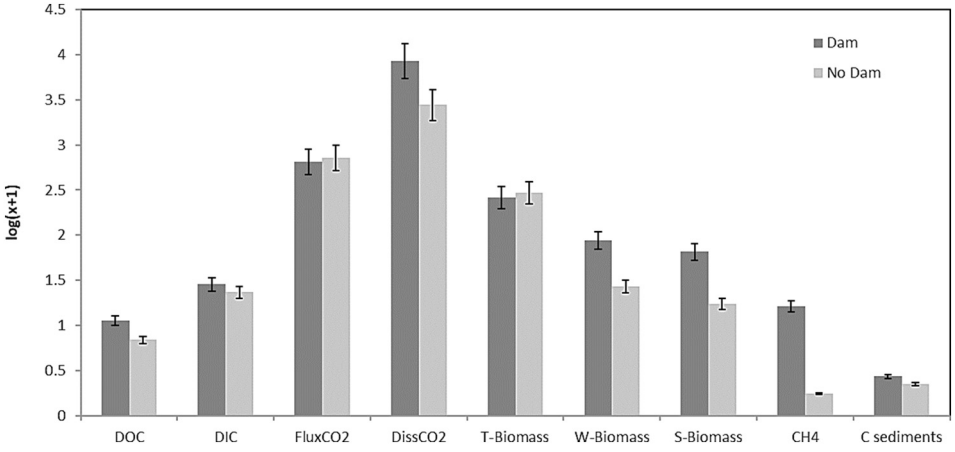

Fig. 3. Comparison histograms of the analysed carbon-related parameters for streams with and without dams ($n = 21 = 7 \times 3$); values are in $\log_{10}$; bars are ±standard error; Biomass S is "shoreline", T is "terrestrial", and W is "aquatic"; $DissCO_2$ is water dissolved carbon dioxide; see the text for other abbreviations; $DissCO_2$, dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC) units of measurements are in ppm; biomass is measured in $g_{dry\ weight}/m^2$, CH_4 in μmol/l, C sediments in $\%/g_{dry}$ and CO_2 flux in $\mu mol/m^2\ s^1$.

activity) increases autochthonous primary production in lakes, promoting oxygen consumption and anaerobic decomposition in the sediments. This can lead to increased CH_4 and CO_2 release from lakes to the atmosphere (Huttunen et al., 2003). By creating physical barriers in streams which slow down the water flow rate, beaver dams increase anoxia in eutrophic lakes which favours CH_4 and CO_2 production (Liikanen and Martikainen, 2003). This increases the residence time of C in water reservoirs and promotes the accumulation of nutrients and allochthonous biomass. We assume that the accumulation of organic carbon and overall atmospheric CO_2 drawdown in pond sediments are proportional to C concentrations and stocks in the sediments, although special measurements of C burial rates might be needed to confirm this hypothesis.

Some of our results from a comparison of carbon-related and ancillary biogeochemical parameters between streams with and without dams in the River Ob floodplain are consistent with previous research on beaver effects in North America (Ford and Naiman, 1988; Yavitt et al., 1992; Bubier et al., 1993; Persico and Meyer, 2013; Wohl, 2013). However, in this study, some new intriguing patterns have emerged. Although we now have the first evidence that methane and dissolved carbon dioxide are about twenty and three times higher, respectively, in western Siberian beaver ponds than in free streams, we do not find a correspondingly higher rate of CO_2 flux. Furthermore, our study shows that the amount of dissolved organic carbon (DOC) and carbon accumulated in the sediments is almost two times higher in dammed streams than in beaver-free ones. As such, beaver dams may act as sizeable sinks of carbon from surrounding ecosystems of the lake watershed. This represents a new important result for a more comprehensive understanding of the full C-cycle in these inland water systems.

4.2. DOC pattern and organic matter benthic accumulation in beaver ponds

It is known that the DOC is not a good indicator for CH_4 production because it contains fulvic acid that is unavailable to methanogens (Ding et al., 2005). In a study of a subtropical lake in China, no relationship was found between methane emission and DOC (Xing et al., 2005). In contrast, in many boreal and temperate lakes, CH_4 production is believed to be most closely related to processing of allochthonous carbon in sediments (Riera et al., 1999; Singh et al., 2000). In 75–95% of the northern and temperate lakes where the atmospheric emissions were supported by the input of terrestrial organic matter (Del Giorgio et al., 1999), a positive relationship between CO_2 flux and DOC was reported. In the River Ob floodplain, we found a higher level of DOC in boreal beaver ponds than in flowing streams but, in contrast to previous studies, no significant ($P > 0.05$) difference in CO_2 emission fluxes. Note that the flux of CO_2 in beaver ponds is about the same as in non-dammed water bodies, while the concentration is about three times as large.

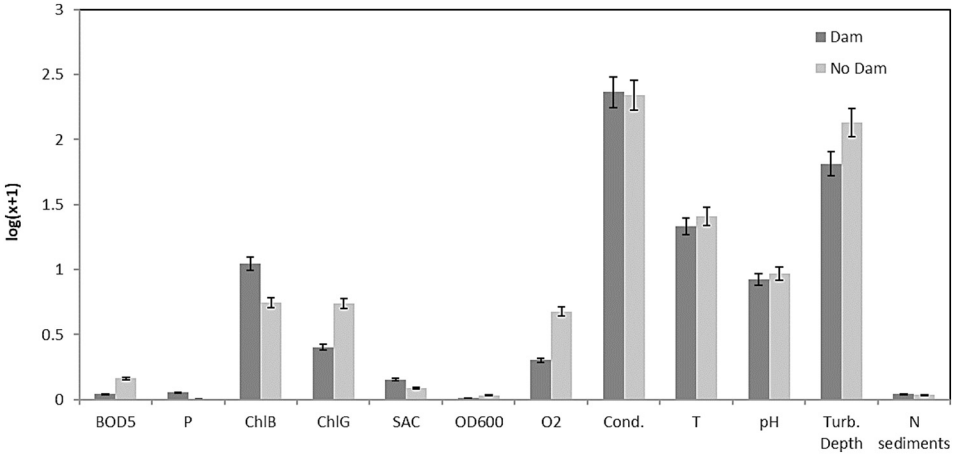

Fig. 4. Comparison histograms of the analysed ancillary parameters for streams with and without dams (values are in $\log_{10}$; bars are ±standard error; see the text for abbreviations; units of measurements: Biological Oxygen Demand (BOD), mg/l; chlorophyll (green and brown algae), μg/l; T, °C; O_2, mg/l; depth of turbidity, cm; optical density $(OD)_{600\ nm}$; conductivity, μS/cm and Spectral Absorbance Coefficient (SAC), abs/m; phosphorous, mg/l; nitrogen $\%/g_{dry}$).

This may be linked to multiple processes affecting the overall gas fluxes to the atmosphere, such as ebullition and wind-dependent emission. In this study, only diffuse fluxes were assessed, which certainly represent only a part of overall GHG emissions from the water surface. Because dissolved oxygen and green algae chlorophyll concentrations are low in beaver ponds we exclude the possibility of an increase of dissolved CO_2 (and thus, DOC) due to higher in-site photosynthetic rate. In fact, the groundwater influx in the flood lakes and streams of the River Ob was demonstrated in a previous study (Vorobyev et al., 2015). As a result, the higher production of CO_2 and DOC would be a consequence of higher organic matter accumulation in the sediment of dammed sites. There, part of the benthic POM is respired (emitting CO_2) and the most recalcitrant part is leached to the lake water in the form of DOC.

In contrast to artificial dams, which are waterproofed and cemented, beaver's ponds are made from natural materials and preserve an intact sediment layer on their bottom (Law et al., 2017; Gorczyca et al., 2018). This allows carbon to accumulate in the sediments and be removed from the short-term biogeochemical cycle. We found that the carbon concentration in the sediments of dammed streams is about twice that of beaver-free streams. This value can be compared with an opposite trend in which there was higher methane concentration in beaver's ponds. In fact, although beavers create similar conditions to artificial dams that increase GHG emission into the atmosphere, they sequester a higher quantity of carbon in the sediments of their ponds. Furthermore, by building their dams, they reduce nutrient (P and N) loss in the waterflow that, in turn, sustains a higher shoreline plant biomass and, probably therefore, carbon draw-down. In the net carbon balance of these inland water systems, these storage effects may compensate, at least partially, the enhanced amount of methane released in beavers' streams.

4.3. C-cycle in beaver ponds

A graphical representation of the carbon-related processes in floodplain streams is shown in Fig. 5. We suggest that, in ponds created by beaver dams, the accumulation of biomass (mainly through a blocked stream water flow) forms particulate organic matter (POM) that is initially decomposed into dissolved organic matter (DOM). The DOM is then further hydrolyzed and fermented; this accounts for most of the DOC and part of the dissolved inorganic carbon (DIC) that can be stored in the water column and sediment. The decomposition of POM into DOM releases into the water a high quantity of phosphate (PO_4^{3-}), which becomes immediately available for biological processes, and nitrogen which accumulates in the sediments. Then, the dissolved carbon is partially released and lost in the water flow. However, a significant percentage is also stored in the bottom sediments and removed from a short-term carbon cycle as DOC. Moreover, under the action of bacteria, DOM may undergo additional fermentations that generate CO_2. Finally, in anoxic conditions, the methanogens could convert CO_2 to CH_4. It has been shown that, in the marine environment, the microbial carbon pump could transform the organic carbon into recalcitrant DOC that resists further degradation and is sequestered for thousands of years (Buchan et al., 2014). We speculate that the formation of recalcitrant DOC by the microorganisms could play a similar role in the sedimentation of organic carbon in beaver ponds. This assumption is supported by our results on the Spectral Absorption Coefficient (SAC 254 nm wavelength), which is a proxy of recalcitrant aromatic carbon content, that was twice greater in beaver ponds.

5. Conclusion

In this study of small streams in the flood plain of the River Ob (western Siberia), we demonstrate that beaver dams increase the quantity of methane that can be emitted into the atmosphere. This is of concern in a world dominated by human greenhouse gasses emissions. At the same time, we show the dominant role of Eurasian beavers in favouring the release of nutrients by increasing the efficiency of the utilisation of dissolved organic matter and in storing carbon in river and stream sediments. Without the presence of this ecological engineer, most of the immobilised nutrients would flow away into the main river channel through long distance river transport and become unavailable for local ecosystems. For instance, the enhanced availability of phosphates and higher concentration of nitrogen in the sediments could be the reason for the four times higher shoreline plant biomass that we found in beaver ponds than in undammed streams. Unfortunately, a full C mass balance with the GHG emission potential of the studied lakes and streams cannot be constructed at present due to lack of data on i) CH4 diffusion and ebullition fluxes, ii) C burial rate in sediments, and iii) quantification of dammed streams and lakes areas in the River Ob flood plain zone.

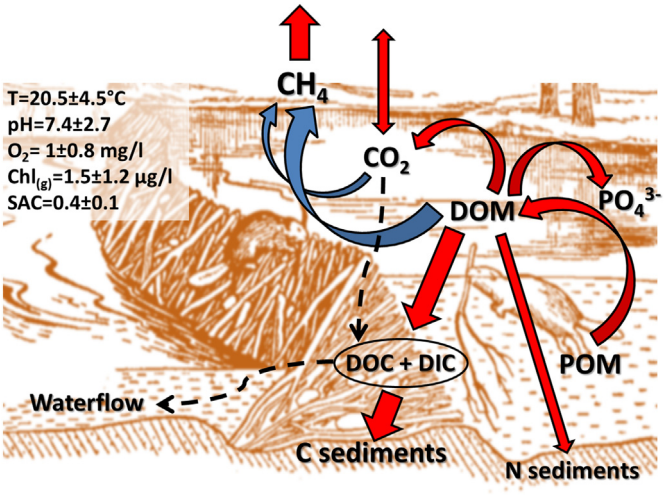

Fig. 5. A summary graphic of carbon compound transitions and pathways in ponds created by beaver dams. The dimension of the arrows indicates the magnitude of the process. Red arrows are both aerobic and anaerobic processes and blue arrows are anaerobic processes only. The strength of the relation between CO_2 and DOC is still debated. Mean values ± standard deviation of the significant parameters recorded in the beaver ponds of the River Ob are reported in the figure.

Moreover, it is still unclear why beavers select a specific stream to dam than another similar one. Tree availability, water depth, channel interconnection, and distance from human infrastructure can be some reasons. However, did the differences between beaver ponds and undammed streams exist before the beavers selected the sites where they built the dam? Only enclosure experiments would confirm this issue and would offer a future opportunity to better interpret our results.

We conclude that, being well-known “ecosystem engineers”, the beavers act as a catalyser (Cazzolla Gatti et al., 2017; Cazzolla Gatti et al., 2018) for the C-cycle in the River Ob flood plain, fostering the feedbacks on the emission/storage rate of streams and oxbow lakes. This should be taken into consideration in river management and as a further reason for the conservation of beaver species. We suggest that the current idea that beavers constitute a major nuisance species in many parts of the northern hemisphere should be rethought. Tree cutting is undesirable to landowners and dam building could result in flooding forests, farm lands and roads. Nevertheless, besides their demonstrated importance in creating new freshwater ecosystems and increasing the local biodiversity, we showed that beavers are a key element in the freshwater C-cycle. Their elimination might cause a cascade effect on the global scale much more negative than that on a local scale, particularly considering their widespread distribution in Eurasia and North America.

Author contributions

RCG conceived and designed the experiments. RCG, IRT and AD performed the experiments, collected and analysed the biological data. AD, AL, SNV and OSP analysed the chemical data. OSP and SNK supported the logistics in the field. RCG, OSP and TVC wrote and revised the manuscript; OSP and TVC provided editorial advice.

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